

The relative importance of prey density and social dominance in determining energy intake by bears feeding on Pacific salmon

S.M. Gende and T.P. Quinn

Abstract: We quantified foraging behavior of brown bears (*Ursus arctos*) feeding on adult chum (*Oncorhynchus keta*) and pink salmon (*Oncorhynchus gorbuscha*) at three small coastal streams in southeastern Alaska from streamside tree stands. These observations revealed that social dominance was much more important in determining intake rates among bears than salmon densities. Each small stream supported one large, socially dominant bear that directly displaced other bears in aggressive encounters or was avoided in “passive deferrals”. Although the number of fish killed per foraging bout was positively correlated with salmon density, energy intake was determined primarily by foraging effort, as dominant bears visited the stream more often and foraged for longer periods than subdominant bears. Capture efficiency (fish captured per minute searching) was highly variable and increased only marginally with salmon density and among social ranks. Subdominant bears were more vigilant, used a smaller fraction of each stream, and carried salmon much farther into the forest prior to consumption, presumably to minimize interactions with other bears. Social dominance may play an important role in regulating reproductive success when salmon densities are low and may have important implications for managers in bear-viewing areas.

Résumé : Nous avons fait, à partir de boisés riverains, une étude quantitative du comportement de recherche de nourriture de grizzlis (*Ursus arctos*) qui se nourrissent de saumons kéta (*Oncorhynchus keta*) et de saumons roses (*Oncorhynchus gorbuscha*) dans trois petits cours d'eau côtiers du sud-est de l'Alaska. Nos observations indiquent que la dominance sociale est un facteur explicatif beaucoup plus important des taux d'ingestion des grizzlis que la densité des saumons. Chaque petit cours d'eau abrite un ours socialement dominant de grande taille qui chasse les autres grizzlis lors de rencontres agressives ou qui est évité par eux par des « soumissions passives ». Il y a une corrélation positive entre le nombre de poissons tués par épisode de recherche de nourriture et la densité des saumons; cependant, l'ingestion d'énergie est surtout déterminée par l'effort de recherche de nourriture, car les grizzlis dominants visitent le cours d'eau plus fréquemment et recherchent leur nourriture pendant une plus longue période que les grizzlis subdominants. L'efficacité des captures (nombre de poissons capturés par minute de recherche) varie considérablement et n'augmente que faiblement en fonction de la densité des saumons et du rang social. Les ours subdominants sont plus vigilants, ils utilisent une fraction plus réduite de chacun des cours d'eau et ils apportent les saumons plus loin dans la forêt avant de les manger, sans doute pour minimiser les interactions avec les autres grizzlis. La dominance sociale peut donc jouer un rôle significatif dans le contrôle du succès reproductif, lorsque les densités de saumons sont faibles; elle a aussi des conséquences importantes sur la gestion des sites d'observation des grizzlis.

[Traduit par la Rédaction]

Introduction

Social dominance has been associated with foraging in many taxa. Dominant individuals tend to get priority access to food (Appleby 1980; Goss-Custard 1980; Baker et al. 1981; Tilson and Hamilton 1984; Monaghan and Metcalfe 1985; Gese et al. 1996; Stahl et al. 2001), forage on higher quality prey (Hupp et al. 1996), have longer foraging bouts (Daily and Ehrlich 1994), spend less time in vigilance (Knight and Knight 1986; Waite 1987), forage under less risk of predation (Schneider 1984; Hegner 1985), and ultimately achieve greater energy intake (Baker et al. 1981;

Metcalfe 1986). Yet the realized foraging advantage associated with social dominance also depends on the abundance and distribution of food. For example, when food becomes more clumped in space and time, it becomes more defensible, resulting in greater variability in allocation among individuals (Theimer 1987; Hupp et al. 1996; McCarthy et al. 1999). Thus, prey-related variation, such as density, as well as variation among predators, such as social rank, will simultaneously influence intake rates, so it is necessary to consider both when studying foraging behavior of predators. Indeed, recent reviews of predator-prey relationships have called for more studies describing both prey- and predator-

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S.M. Gende.¹ National Park Service, Glacier Bay Field Station, 3100 National Park Road, Juneau, AK 99801, U.S.A.

T.P. Quinn. School of Aquatic and Fishery Sciences, Box 355020, University of Washington, Seattle, WA 98195, U.S.A.

¹Corresponding author (e-mail: Scott_Gende@NPS.gov).

related variation (Abrams and Ginzburg 2000), particularly when prey are spatially constrained (Cosner et al. 1999).

Bears and salmon

Every year from late summer through the fall, brown bears (*Ursus arctos*) and black bears (*Ursus americanus*) congregate in riparian areas to feed on Pacific salmon (*Oncorhynchus* spp.), which return to freshwater streams to spawn and die. This predator–prey relationship provides an excellent opportunity to study the simultaneous role of food density and social dominance in determining individual intake rates for a large free-ranging omnivore for several reasons. First, the opportunity to feed on salmon has direct fitness benefits and costs for bears. Salmon are relatively high in energy density compared with alternative foods (Welch et al. 1997; Rode et al. 2001) and become available in the late summer and early fall when it is necessary for bears to put on sufficient layers of fat to fuel metabolic and reproductive costs while denning. Bears will lose 30% or more of their body reserves while fasting in the dens because lipid stores are used to fuel reproductive (birth, lactation) and metabolic activities (Hilderbrand et al. 2000). Consequently, the reproductive success of female bears has been linked to body condition prior to den entrance (Rogers 1987; Stringham 1989; Atkinson and Ramsay 1995; Samson and Hout 1995). However, the energetic benefits of salmon consumption may be offset by social costs associated with foraging. Many cases of intense agonistic interactions among bears, resulting in serious wounds and death (to combatants or their offspring), have been recorded at salmon streams and other clumped food resources (Luque and Stokes 1976; McLellan 1994; Chi 1999). Social costs may be so great that some bears may choose to forage in less productive but safer habitats, such as alpine areas, and forego the opportunity to utilize salmon (Schoen et al. 1986; Hilderbrand et al. 1996). In Yellowstone National Park, female bears that utilized trout streams lost a greater proportion of their dependent young compared with females that foraged elsewhere, presumably because of greater intraspecific predation associated with the bear congregations at streams (Mattson and Reinhart 1995).

Second, salmon densities can be easily quantified because they are spatially and temporally clumped, returning to spawn in small streams with little variation in timing of returns. The number of fish returning to spawn also varies naturally among streams and within a stream among years (Quinn et al. 2003), resulting in differences in densities encountered by bears. Finally, energy intake for bears feeding on salmon can be accurately estimated because bears generally carry captured salmon from the stream to a gravel bar or into the forest where they are partially consumed (Gende et al. 2001). The amount of tissue consumed from each carcass can be estimated by measuring the lower jaw, body length, and carcass mass and applying species- and sex-specific lower jaw – body mass or body length – body mass relationships established from live fish (Gende et al. 2001). Tissue-specific energetic values can then be applied to the estimates of biomass consumed, resulting in an accurate estimate of the total energy intake for each individual for each foraging bout.

Our overall objective was to examine the relative influences of salmon density and social dominance on energy in-

take rates by bears by observing bears fishing for salmon in pristine riparian systems. We tested the hypothesis that salmon intake (including the number of fish killed per bout) capture efficiency (salmon captured per minute searching), and energy intake (kilojoules per foraging bout) would all increase with increasing salmon density and that dominant bears would have higher rates of intake than other bears after accounting for differences in salmon density. We also hypothesized that effort, defined as foraging bout duration, would increase with increasing salmon densities, as opportunities to capture fish increased. Dominant bears were predicted to have longer foraging bouts, but subordinate bears were hypothesized to compensate for lost foraging opportunities (when displaced by dominant bears) by visiting the streams more often.

Methods

Study sites

Our study streams are on northeast Chichagof Island about 70 km west of Juneau, Alaska (58°21'N, 134°36'W). These sites were relatively free of anthropogenic influence and supported healthy populations of salmon (Halupka et al. 2000) and bears (Beier et al. 1996). Many of the published and publicized observations of bears fishing for salmon have occurred at the McNeil River Falls (e.g., Sellers and Aumiller 1994; Olson et al. 1997) and Brooks Falls in Alaska. These sites are unusual because salmon availability is concentrated at waterfalls (deep water prohibits successful fishing elsewhere) that salmon negotiate on their migration to spawning sites farther upriver. Bears must obtain one of a limited number of fishing sites at the falls, and this concentrates many bears in an unusually small area. In contrast, many of the over 4000 freshwater systems where salmon spawn in southeastern Alaska are small, low-order streams (Halupka et al. 2000) where bears can walk much of the stream and forage on spawning salmon in a less limited area. Thus, our sites more closely represent the typical situation where bears feed on salmon across their range.

The three streams that we selected for this study varied in physical characteristics, but all were shallow, had ≤ 1 km of suitable spawning habitat, had alternating riffles and pools, and flowed directly into the ocean over an intertidal reach. Bear Creek and Himmel Creek were similar in size (wetted channels about 4.5 m wide). Both creeks had several pools that were 1–1.5 m deep, but most of the spawning occurred in riffles 0.3–0.5 m deep. Bear Creek had about 540 m of spawning habitat, the upper extent ending at a large woody debris jam. Himmel Creek's accessible length differed between years. In 1999, fish spawned only in the lower 330 m of the stream because further access was limited by a debris jam. The debris jam was washed out during the next winter, and in 2000, fish had access to almost 1 km of spawning habitat, although most of the fish spawned in the lower 300 m. Lake Creek, the smallest of the three study streams, had several narrow channels and a large intertidal area where spawning occurred. The riparian areas of all three streams were characterized by old-growth Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*) and an understory of shrubs and grasses.

Bear Creek and Himmel Creek supported runs of chum salmon (*Oncorhynchus keta*) and pink salmon (*Oncorhynchus gorbuscha*), whereas Lake Creek had only pink salmon. Salmon of both species began shoaling near the entrance of the creeks (in salt water, where they are unavailable to bears) in late July and early August. Chum salmon began entering the streams in late July, and pink salmon entered 2–3 weeks later (also see Dickerson et al. 2002). During the first few days of the spawning season, most of the fish were concentrated in the lower sections of the stream, but the salmon then dispersed and spawned throughout the accessible reaches of the streams, including intertidal areas.

The general life history of pink and chum salmon in these streams (and many similar streams nearby) is as follows. Both species stop feeding and become sexually mature prior to entering freshwater. Soon after they enter streams, salmon begin courtship, nest construction, and spawning. Females deposit their eggs in the gravel after 1–4 days, and all salmon die of senescence (unless killed by bears) after 10–20 days in the stream (Dickerson et al. 2002). The salmon carcasses then settle in pools, get caught up on large woody debris, or drift downstream where they accumulate on gravel bars until freshets or high tides carry them out to the ocean. Over the course of their in-stream life, salmon lose energy (primarily lipid and protein) precipitously. Both species utilize stored energy reserves to fuel spawning and metabolism and die having lost nearly 90% of their lipid reserves and a significant amount of protein (Gende et al. 2004).

Foraging observations

We observed bears from small (1.0 m × 0.7 m) tree stands placed in large coniferous trees 21–30 m above the stream. Observation periods in tree stands began the day salmon first entered the stream in 1999 and 2000 and continued into late September during the latter stages of the salmon run. Heavy precipitation in September elevated stream flows and bear activity declined sharply. Observation periods generally lasted 7–12 h and began between daybreak and midday. For many days, we had multiple observation periods within a stand, where one observer would record foraging behavior from the early morning until midafternoon and another observer would record behavior from midafternoon until late evening, thus encompassing most of the day (because of the long days, darkness prohibited observations for only a few hours). Preliminary observations in 1998 and the early part of 1999 revealed that most foraging activity occurred in the late afternoon and early evening (also see Frame 1974; Luque and Stokes 1976; Klinka and Reimchen 2002), so to maximize the amount of behavior observed, most observation periods began in the late morning and ended at twilight. To minimize interobserver variation when recording behavior, nine foraging bouts videotaped in 1998 and 1999 were used to train observers before fieldwork began.

To minimize the possibility of detection, tree stands were placed in trees several weeks before salmon and most bears arrived. Streams were accessed by a boat, which was moored, on average, 1.3 km from the stream mouth. To minimize our scent, we wore rubber boots, raingear, and rubber gloves (when measuring bear-killed salmon) and accessed the tree stands by walking in the intertidal area and on streamside gravel bars. We avoided touching streamside veg-

etation when possible, except when climbing to the tree stands.

Tree stands were located to maximize the observable area of the stream and where salmon spawning (and thus, most bear activity) occurred. At Bear Creek and Himmel Creek, tree stands were located in both the lower and upper reaches of the stream, with most of the spawning area within sight from the two tree stands. However, because of the meandering nature of the stream and overhanging vegetation, some sections of the stream were out of sight from some tree stands. Consequently, we were unable to observe some foraging bouts in their entirety. These partially observed bouts were noted because they represented only partial estimates of intake, and these data were used only when calculating rates (e.g., fish caught per minute searching). However, in most cases, we observed the entire foraging bout.

We were confident that the bears were unaware of (or unaffected by) our presence for two reasons. First, most of the foraging bouts occurred in the stream sections near or under the tree stands, with bouts often lasting 60 min or more. Second, there were several instances when foraging bears reacted to some other human presence that was much farther away (e.g., motorized boat or kayak out in the ocean passing near the stream) by standing and sniffing in the direction of the disturbance or rapidly walking off the stream. However, despite our precautions, on several occasions, bears stopped foraging and sniffed in the direction of the tree stand (particularly on windy days), suggesting that they may have detected the observers. Even though the bears often continued foraging, these bouts were excluded from analysis.

Whenever a bear was observed using the stream, we used binoculars and voice-activated audio recorders to log the following data: bear identification, foraging bout duration (not including approach or exit), number of attempts at catching salmon, and number of fish killed or scavenged. Identification of individual bears (no more than eight per stream) was facilitated by a combination of distinguishing scars or pelage, body size, ear tags or radiocollars (previously attached by Alaska Department of Fish and Game personnel), reproductive status (e.g., number of cubs present), and distinguishing behavior (also see Fagen and Fagen 1996). A running description of each bear was kept at the field camp and updated daily. We classified a foraging attempt (an attack) as any lunge at a fish while standing in the stream or pursuit involving rapid steps (walking, running) culminating in a lunge at a fish. Bears primarily caught salmon by putting their mouths in the water and grasping the fish in their jaws or pinning the fish to the stream bottom with their front paws, so these lunges were quite unequivocal to classify. Bout duration was separated into time spent searching, carrying, feeding, and other activities. Search time began when bears reached the stream and were looking into the water and continued until a salmon was captured. Carrying time was the time from capture until the bear started to feed on the fish or released it. Feeding included the time from first bite until the carcass was abandoned. Other activities (e.g., frugivory, interactions with other bears) were combined into a single category and represented a very small fraction of the total time on streams.

To quantify intake for a bear during a bout, we mapped the ultimate location of each carcass (94% of the 882 ob-

served salmon captures were carried to a gravel bar or into the forest to be consumed). Following each observation period, we located the carcasses and recorded the distance the carcass had been taken from the stream and the salmon's species, sex, spawning status, and body parts consumed (e.g., gonads, brain; see Gende et al. 2001). We also recorded the length of the lower jaw and (when possible) body length (mid-eye to hypural plate). We estimated the biomass consumed from each carcass by taking the difference between the carcass mass (remaining tissue) and the expected original mass (prior to consumption) based on lower jaw – body mass and body length – body mass relationships (see regression parameters in Gende et al. 2001). If neither body length nor jaw length could be measured, we estimated intake based on body parts consumed (Gende et al. 2001). Energy intake was then calculated (in kilojoules wet mass) by multiplying mass-specific energetic content of each body part (Gende 2002) by the amount of biomass consumed, summed over all fish killed or scavenged during that foraging bout.

We also recorded the frequency of vigilance behavior because this activity may reduce intake rates, as seen in other species (e.g., Knight and Knight 1986; Waite 1987). Bears often become vigilant by standing on their hind legs (bipedal behavior) and looking and sniffing in the direction of a perceived threat. We recorded the frequency of such bipedal behavior by each bear for each bout as an index of vigilance. Bears undoubtedly exhibit other, more subtle forms of vigilance (e.g., looking around while feeding), but these behaviors might not always reflect vigilance and so were not used for this purpose.

We used time as an indicator of effort because (i) time spent fishing for salmon could have been spent searching for alternative food resources (e.g., berries, carrion), (ii) longer foraging bouts increase the probability of agonistic interaction with other bears, and (iii) accurate estimates of activity-specific energy use (e.g., running, walking, etc.) are not available (C.T. Robbins, Washington State University, Pullman, Wash., personal communication).

Fish densities and social interactions

To measure fish densities, each stream was divided into reaches according to natural changes in geomorphology. Stream width was recorded for each reach at 10 equidistant points on several occasions during the run, when precipitation dramatically altered flow levels. Spawning salmon were counted during each visit to a tree stand and density was estimated for each reach by dividing the count by the area (i.e., salmon per square metre). We used salmon per stream area, rather than per volume of water (salmon per cubic metre; Mattson and Reinhart 1995), because salmon densities are generally calculated per area of stream (Quinn and Kinnison 1999; Quinn et al. 2003) and the streams were shallow enough that the fish were distributed in two dimensions rather than three. However, analyses using salmon per volume of water were identical to results when using area, so no conclusions were affected by this metric.

We also recorded the outcomes of interactions between bears when they were seen on the stream simultaneously. Some interactions between bears were direct, with one bear

aggressively walking or running toward the other and actively displacing it from the stream. However, many interactions resulted in “passive deferrals”, when one bear (presumably the subordinate) deferred to another (dominant) individual by maintaining a minimum distance between itself and the other bear (Chi 1999) or by moving when the dominant bear walked or foraged in its direction.

Although there were consistent winners and losers in the interactions among bears, the small number of interactions that we observed (relative to the total number of possible interactions) hindered our ability to accurately quantify social status for all bears. For example, in 2000, we observed 38 interactions among bears and these constituted from 33% (at Lake Creek) to 24% (at Bear Creek) of the possible dyadic interactions. In 1999, the percentages were even lower because we observed only 29 interactions, mostly at Bear Creek. Therefore, we could not establish the social rank of every bear at each site in each year. Nevertheless, each stream appeared to support an individual that won 100% of its interactions and thus was labeled “dominant” (Drews 1993). We also observed that some bears always deferred to other bears (subordinate in 100% of their interactions). We labeled these bears as “subordinate” if they had at least four interactions with other bears and they deferred in all interactions. Finally, we labeled all other bears as “intermediate” because they always deferred to the dominant individual but often exhibited circularity when interacting with other bears (A defers to B, B defers to C, C defers to A). There was probably some degree of social order among the intermediates, but the data were inadequate to support further refinement in status categories.

Although this method of ranking status (dominant, intermediate, subordinate) was simplistic compared with several other methods used to establish dominance hierarchies among social animals (e.g., de Vries and Appleby 2000; Albers and de Vries 2001), we opted to avoid possible spurious rankings based on interactions that we did not observe and simply compared intake rates of bears that were clearly dominant with intake rates of intermediates and subordinates. Because interactions were so infrequently observed at Himmel Creek and Lake Creek in 1999, we excluded these data when comparing foraging behavior among social classes.

Data analysis

We used analysis of covariance (ANCOVA) (PROC GLM, SAS Systems Inc., Cary, N.C.) to test for differences in the regressions among social classes (dominant, intermediate, or subordinate) of foraging efficiency (fish captured per minute foraging), energy intake (kilojoules intake per foraging bout), and effort (foraging bout duration) relative to salmon density (fish per square metre). To test for heterogeneity in slopes, we first ran the ANCOVAs with an interaction term (social status \times fish density) and if this term was insignificant (demonstrating that the relationships between intake and effort with fish density were similar regardless of social status), we reran the ANCOVAs without the interaction term to test for differences in the adjusted means (intercepts).

For these analyses, we used each bout as a data point. This approach allowed us to consider the intake and foraging effort of bears differing in social status at different salmon

densities. Because there were multiple observations of the same bear over the course of the season (i.e., at different salmon densities), the data points were not independent. However, the amount of variation among bouts by individual bears was consistently larger than the variation among bears (PROC VARCOMP, SAS Systems Inc.). For example, 63% of the variation in energy intake relative to fish density was attributed to variation among bouts within bears for intermediates and subordinates and 91% for dominant bears. This approach underestimates the probability of Type I error but is the best way to examine foraging by scarce animals such as bears (e.g., species for which there are too few individuals for statistically powerful analysis using each animal as the unit of replication). Our data are less likely to suffer from a lack of statistical independence than the main alternative approach, which typically uses one or two captive bears and experimentally manipulates food densities (e.g., Welch et al. 1997; Hilderbrand et al. 1999b; Rode et al. 2001).

Having first considered variation among foraging bouts, we then considered variation among bears by averaging intake and effort for each bear across years and fish densities. For each of these analyses, we had no a priori hypotheses of the distribution of the data (e.g., asymptotic, quadratic, etc.), so we used simple linear regression in each case. Statistical significance was considered at $P < 0.05$.

Results

During 132 observation periods in trees stands (842 h of observation), we observed 240 foraging bouts: 9 bouts during preliminary observations in 1998, 85 in 1999, and 146 in 2000. Of all foraging bouts, 172 (72%) were seen in their entirety: 8 in 1998, 60 in 1999, and 104 in 2000. We excluded 37 foraging bouts from our analysis because the foraging behavior of bears was apparently modified by some human activity (e.g., detection of observer, floatplane in the area, boat near the shore). In addition, we were unable to collect data on some parameters (such as fish density) during some foraging bouts, further reducing the sample sizes available for some analyses.

The number of bears using each stream varied little between years. We identified eight bears using Bear Creek in 1999 and seven bears in 2000, four of which had been seen in 1999. Similarly, five bears were seen at Himmel Creek in 1999 and 2000, and three of them were seen in both years. Seven bears were seen at Lake Creek in 2000, but we did not visit Lake Creek enough in 1999 to accurately establish the total number of bears using this stream.

The number of live salmon killed per foraging bout increased significantly with salmon densities, but capture efficiency and energy intake were generally independent of salmon density (Table 1, Fig. 1). Tests for heterogeneity of slopes were insignificant for each ANCOVA, so they were rerun without the interaction term (Table 1). Comparisons of adjusted means (i.e., accounting for salmon densities) among social classes indicated that dominant bears killed over twice as many live salmon per foraging bout as intermediates (mean number of live salmon captured per bout, 6.9 ± 0.52 versus 3.2 ± 0.56 , $P < 0.001$) and subordinates (2.6 ± 0.83 ,

Table 1. ANCOVA testing for differences in number of live fish killed, capture efficiency, foraging bout duration, and energy intake per bout relative to chum (*Oncorhynchus keta*) and pink salmon (*Oncorhynchus gorbuscha*) density for dominant, intermediate, and subordinate brown bears (*Ursus arctos*).

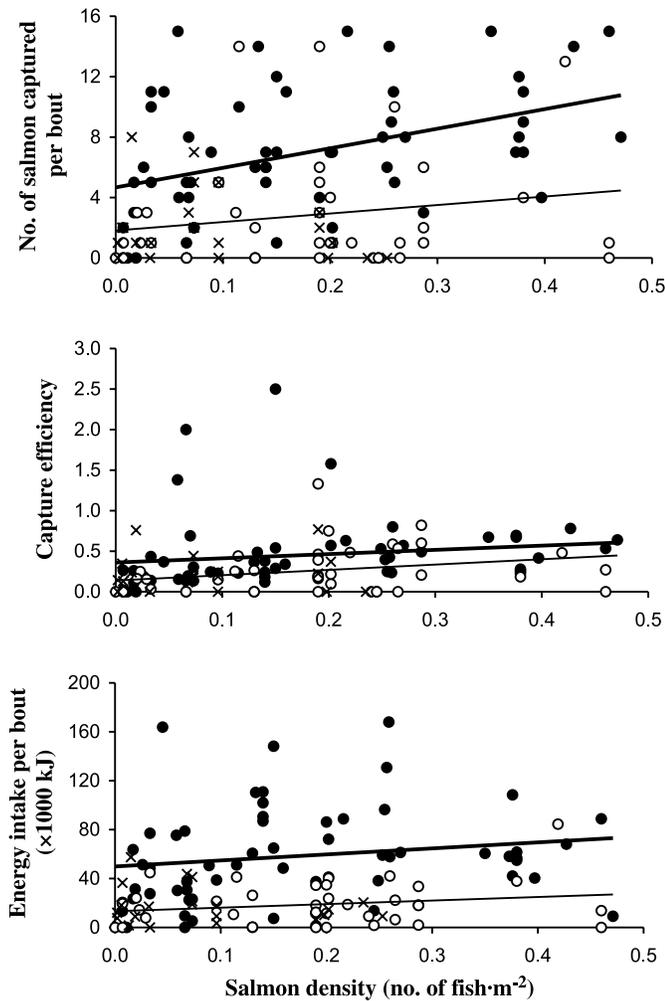
Dependent variable and source	df	F	P
With interaction term (social status × salmon density)			
No. of salmon killed per bout	2	1.48	0.232
Capture efficiency	2	0.03	0.967
Bout duration	2	0.41	0.662
Energy intake	2	0.50	0.607
Without interaction term			
No. of salmon killed per bout			
Salmon density	1	8.98	0.033
Social status	2	16.17	<0.001
Error	116		
Capture efficiency			
Salmon density	1	3.50	0.063
Social status	2	2.93	0.056
Error	143		
Bout duration			
Salmon density	1	0.32	0.572
Social status	2	10.19	<0.001
Error	116		
Energy intake			
Salmon density	1	1.79	0.184
Social status	2	10.96	<0.001
Error	116		

Note: The top section of the table shows the results of testing for slope heterogeneity among the social classes for each relationship. The bottom section of the table shows the results after the interaction term (slopes were similar among social classes) was removed. We included partially observed foraging bouts to estimate capture efficiency, resulting in a larger sample size for this test.

$P < 0.001$); no differences were observed between intermediates and subordinates ($P = 0.614$). However, differences in capture efficiency were only marginally significant between dominant versus intermediate (mean number of salmon captured per minute searching, 0.42 ± 0.05 versus 0.30 ± 0.05 , $P = 0.06$) and subordinate bears (0.23 ± 0.08 , $P = 0.05$); intermediates and subordinates were not significantly different ($P = 0.58$). Dominant bears had almost twice the energy intake per foraging bout compared with intermediates (mean kilojoules per bout, $53\,991 \pm 4531$ versus $28\,482 \pm 4820$, $P = 0.002$) and nearly three times more than subordinates ($20\,637 \pm 7335$, $P = 0.002$); intermediates and subordinates were not different ($P = 0.38$).

The amount of time bears spent foraging (effort) was independent of salmon density (Table 1, Fig. 2), and tests for heterogeneity in slopes also showed that the relationship between bout duration and salmon density did not differ among social ranks. Dominant bears spent almost twice the amount of time on the stream foraging as intermediates (mean bout duration, 46.1 ± 3.5 min versus 28.5 ± 3.7 min, $P = 0.008$) and subordinates (19.2 ± 5.8 min, $P = 0.001$); intermediates averaged over 30% more time on the stream per bout than subordinates but the difference was not significant ($P = 0.19$). Thus, dominant bears, although slightly more efficient, had higher energy intake primarily because they

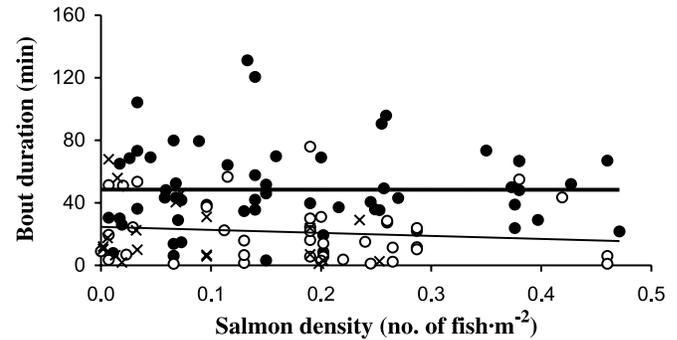
Fig. 1. Intake, including number of chum (*Oncorhynchus keta*) and pink salmon (*Oncorhynchus gorbuscha*) killed per foraging bout, capture efficiency (no. of salmon captured/min searching), and gross energy intake per foraging bout in relation to salmon density for dominant (●), intermediate (○), and subordinate (×) brown bears (*Ursus arctos*) at Bear (1999–2000), Himmel (2000), and Lake creeks (2000), southeastern Alaska. Slopes for each relationship were not significantly different among social classes. Intercepts were not significantly different for intermediates and subordinates, so we plotted these two groups with common slope and intercept.



were able to spend more time on the stream without being displaced, allowing them to capture more fish.

The patterns of vigilance, location of carcass consumption, and amount of stream used also indicated that dominant bears were able to spend more time foraging than other bears. Intermediate and subordinate bears were more often vigilant than dominant bears (Fig. 3), temporarily ceasing to fish and standing on their hind legs to scan the surrounding area every 4.5 min, particularly when foraging in the presence of another bear. Furthermore, dominant bears often walked most of the stream reach during a foraging bout, whereas the movements of other bears were more limited in space (Fig. 3). Although we found no significant difference among social classes in the average distance that carcasses

Fig. 2. Effort, as measured by foraging bout duration, in relation to chum (*O. keta*) and pink salmon (*O. gorbuscha*) density for dominant (●), intermediate (○), and subordinate (×) brown bears (*U. arctos*) at Bear (1999–2000), Himmel (2000), and Lake creeks (2000), southeastern Alaska. Slopes for each relationship were not significantly different among social classes. Intercepts were not significantly different for intermediates and subordinates, so we plotted these two groups with common slope and intercept.

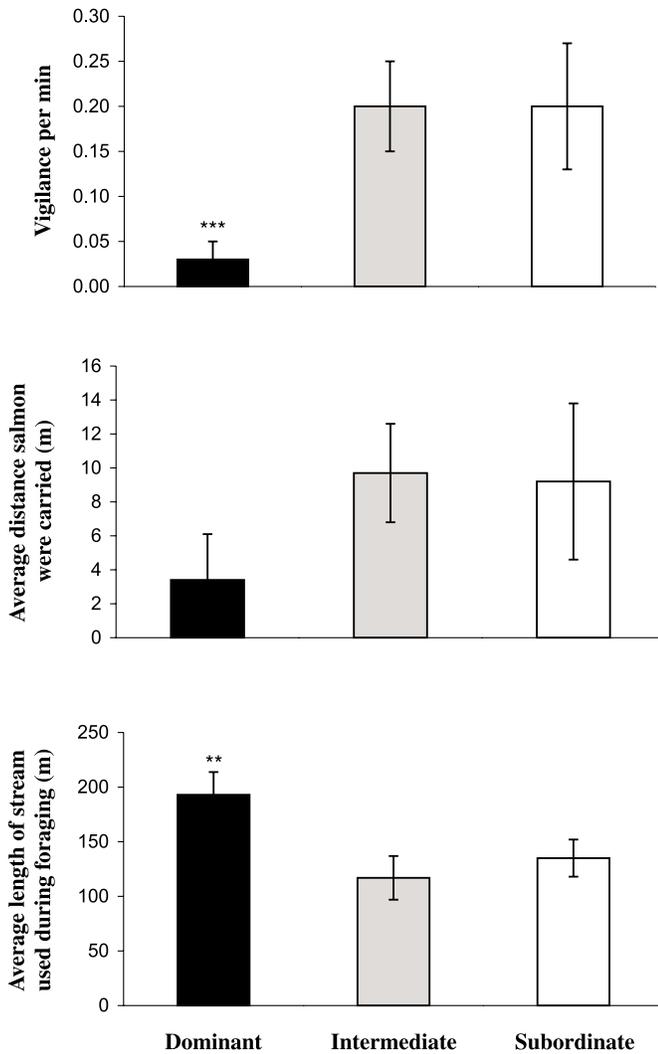


were carried prior to consumption (Fig. 3), intermediate and subordinate bears carried fish almost three times farther than dominant bears. This result does not reveal that, at many sites along these streams, dense vegetation is only 2–4 m from the water's edge across gravel bars and grass. Dominant bears often consumed salmon in open view on the stream bank or gravel bars, whereas intermediate and subordinate bears carried the carcasses away from the immediate stream edge, presumably to reduce the probability of competitive interference. In some cases, subordinate bears carried carcasses more than 200 m from the stream, often to areas with dense vegetation or at elevated sites above the floodplain.

Given that effort was independent of salmon density, we examined the relationship between intake (number of salmon killed, energy intake per foraging bout) and effort (foraging bout duration) by averaging all bouts per individual bear. Here, the data points are individual bears rather than foraging bouts. Not surprisingly, the number of fish killed during a bout and energy intake were strongly correlated with foraging bout duration (Fig. 4). These data also revealed the dramatic differences in average effort and intake among individual bears. For example, at Bear Creek the average bout duration ranged from less than 10 min to 61 min and between 10 000 and 80 000 kJ intake among bears.

Variation in bout frequency further skewed the intake of fish among individuals. If bears that had abbreviated foraging bouts compensated by visiting the streams more often, we would expect that bout duration would be inversely related to bout frequency. In contrast, we found a significant positive relationship between the proportion of total bouts observed and average bout duration (average bout duration = $13.5 + 66.6 \times \text{proportion of total bouts}$; $F = 6.07$, $P = 0.023$, $r^2 = 0.28$). Thus, the dominant bears had longer foraging bouts and also visited the streams more often, resulting in far more energy consumed over the spawning run compared with lower status bears.

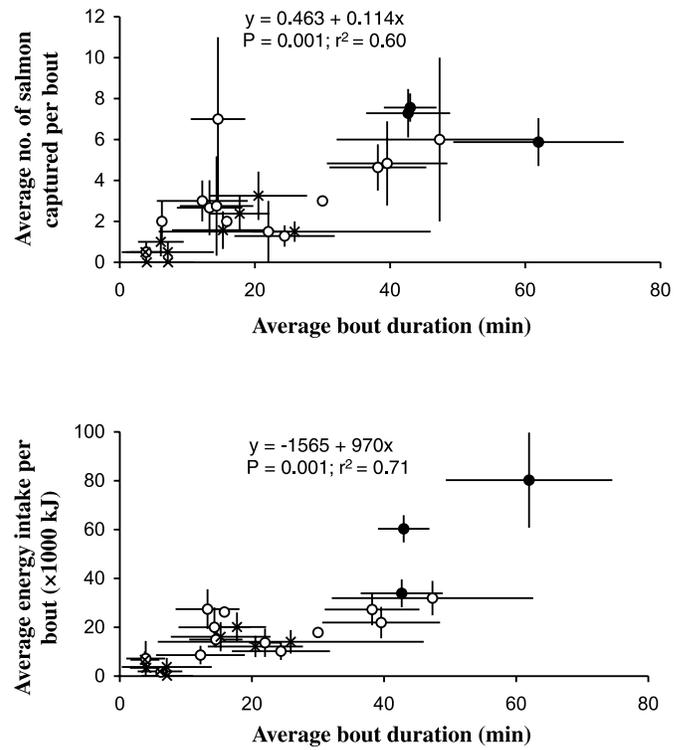
Fig. 3. Average vigilance (bipedal behavior/min foraging), average distance that captured chum (*O. keta*) and pink salmon (*O. gorbuscha*) were carried away from the stream prior to consumption, and average length of stream used during a foraging bout for dominant (solid bars), intermediate (shaded bars), and subordinate (open bars) brown bears (*U. arctos*) at Bear (1999–2000), Himmel (2000), and Lake creeks (2000), southeastern Alaska. Dominant bears were significantly less vigilant and used a significantly greater proportion of the stream (averaged across all foraging bouts) than intermediate and subordinate bears (**, $P < 0.01$; ***, $P < 0.001$).



Discussion

We found little support for our initial hypotheses that energy intake would increase with increasing salmon density. Rather, most of the variation in intake among bears could be attributed to differences in social status. To understand why salmon density was unrelated to intake, it is important to consider the geomorphology of these streams and how it may influence the steps in the predation event, including encounter, attack, and capture probabilities. For example, characteristics of prey, such as morphology and escape behavior, may influence one or several of these probabilities (Sih and

Fig. 4. Relationship between the average number of chum (*O. keta*) and pink salmon (*O. gorbuscha*) killed per foraging bout and average bout duration and between average energy intake and average bout duration for dominant (●), intermediate (○), and subordinate (×) brown bears (*U. arctos*) at Bear (1999–2000), Himmel (2000), and Lake creeks (2000), southeastern Alaska. Each data point represents an individual bear.



Christensen 2001), but prey density typically influences encounter rates because higher prey densities generally provide more opportunities for predators to detect them. Thus, intake should vary with density when density is closely related to encounter probability. However, the ability of bears to encounter salmon was generally independent of salmon density because our study streams, like many other streams in southwestern (Quinn et al. 2003) and southeastern Alaska (Halupka et al. 2000), are quite shallow (mean depth of 0.4 m in riffles, 1.4 m in pools) and narrow (mean wetted width of 4.5 m, although in many areas, 2–3 m of the stream width was too shallow for salmon to adequately maneuver). The primary method that bears used to catch salmon was to walk slowly up the middle of the stream, thereby blocking downstream escape by salmon and forcing them to flee upstream. Consequently, even when only a few fish were present, bears were able to detect (encounter) salmon. Moreover, bears would have little trouble capturing a fish following an encounter because fleeing salmon often swam up shallow riffles to the deeper pools or under tangles of in-stream woody debris. The shallow water did not hinder pursuing bears but often hindered the swimming of salmon. As a result, the probability of capture, given an attack, averaged almost 60%, and bears were able to capture a salmon after only 2.5 min of searching, for all bears across all salmon densities.

In contrast, when water is much deeper, encounter probability is likely to be much more closely linked to changes in salmon density (Gende et al. 2004). For example, the McNeil River Falls is much deeper than these small coastal streams, and bears "encounter" fish primarily when the salmon attempt to leap a barrier falls. Greater runs of salmon navigating the falls lead to elevated encounter rates with bears. Luque and Stokes (1976) noted that capture rates were higher during years of higher salmon densities, suggesting a stronger relationship between intake and salmon density.

That encounter rates were more a function of shallow water than number of fish present was exemplified in the response of bears to two different conditions by which salmon densities were relatively low: (1) low numbers of fish at the very beginning and end of the run and (2) periods when high stream flows followed extended periods of precipitation. For example, the lowest number of salmon recorded at Bear Creek occurred on the first day of the run in 1999, when 14 chum salmon entered the stream. Flows were relatively low, and the dominant bear visited the stream and captured 8 of the 14 salmon, foraging for only 44 min. In contrast, on 22 and 23 August 2000, salmon densities were similar to those seen during the first few days of the run in 1999, not because few fish were present but because flows were much higher following several days of heavy precipitation, increasing the stream area considerably. For these 2 days, we observed two foraging bouts, each by the dominant bear. In each case, the bear walked the stream but made no attacks, ultimately scavenging three fish and leaving the stream after an average of 6 min. The high flows and increased turbidity presumably lowered encounter rates enough that bears opted to forage away from the stream rather than forage when encounter rates were much lower. That stream size is related to predation rates has been demonstrated in several other studies in Alaska, with higher predation rates occurring on salmon that spawn in smaller streams (Quinn and Kinnison 1999; Quinn et al. 2001).

For most of our observations, however, salmon were dense enough that social dominance was far more important in regulating intake than salmon densities. Some level of social dominance has been recorded in nearly every observational study of bears foraging at clumped food resources (Herrero 1983; Rogers 1987; Craighead et al. 1995), including salmon streams (Frame 1974; Luque and Stokes 1976; Warner 1987; Chi 1999). At our streams, social dominance influenced how much time was spent foraging and, because capture efficiency was generally independent of fish density, this directly influenced the number of salmon captured and gross energy intake.

The dominant bears at our streams were all large females, although social rank did not vary with reproductive status. At Bear Creek, a large female was dominant in both years, despite having spring cubs (born the previous winter) in 1999 and yearlings in 2000. She was also regularly avoided by other bears in 1998 when not accompanied by dependent young. This individual was one of the largest female bears in the area, weighing 265 kg when radiocollared by Alaska Department of Fish and Game personnel in 1993. Similarly, a large female was dominant in both years at Himmel Creek,

visiting the stream alone in 1999 (having weaned three 2-year-old cubs earlier in the summer) but with two spring cubs in 2000. At Lake Creek, a fairly large female with two yearlings was dominant in 2000.

For other studies of bears at clumped food resources, dominant bears were always large, but the sex varied (females: Herrero 1983; Chi 1999; males: Luque and Stokes 1976). Surprisingly, we rarely observed large males using our streams. Once at Lake Creek, a large male foraged for 38 min, repeatedly charging a subordinate female with two yearlings, before exiting the stream. Another large male was observed walking across Bear Creek (no foraging attempts were made) and was later seen at a larger creek (Seagull Creek) several kilometres away. Adult males have larger home ranges, perhaps to increase breeding opportunities (Kovach 1998), and may favor larger streams (L. Beier, Alaska Department of Fish and Game, Juneau, Alaska, personal communication).

As a result of the large number of fish captured and relatively long foraging bouts, intake by dominant bears was more likely to be limited by some physiological constraints (gut capacity or nutrient processing rates; Hilderbrand et al. 1999b) compared with other bears. For example, dominant bears killed nearly seven salmon per foraging bout, equivalent to about 24 kg. During feeding trials in captivity, adult brown bears fed salmon ad libitum consumed up to 15% of their body mass, which equates to about 24 kg of salmon per day for an average-sized female bear in this area (160 kg; Titus and Beier 1993). Thus, the total biomass of salmon captured during a single foraging bout (often 60 min or less) by dominant bears far exceeded their daily maximum intake ability. This explains why salmon were partially consumed, with bears targeting body parts, such as the roe in females and the brain in males, which were highest in mass-specific lipid content (Gende et al. 2001; Gende 2002). Dominant bears have the freedom to selectively kill the energy-rich fish (Gende et al. 2004) and selectively consume body parts highest in lipid density (Gende et al. 2001), further elevating lipid intake per foraging bout.

The ability to reach gut capacity also explains why we found strong relationships between effort and intake and why some foraging bouts by dominant bears were terminated after only a few fish were captured. If bears do not wait until all fish consumed during the previous foraging bout are digested before revisiting a stream, only a few salmon would be needed to reach satiation. Many of the foraging bouts by dominant bears, where only several salmon were consumed, occurred during the latter stages of the salmon run (after many days of feeding) or during the second or third foraging bouts observed that day. Bears may thus modify effort according to their degree of satiation during visits to the stream.

Subordinate bears often had intake rates far lower than dominant bears and in many cases exited streams after capturing only a few salmon. There was some evidence, however, that subordinate bears compensated for frequent displacement from the stream reaches by utilizing the intertidal areas when possible. The intertidal reaches of small coastal streams in southeastern Alaska are commonly large, and salmon carcasses often accumulate there before being

washed out to the ocean during the next tidal cycle (Frame 1974). At high tides, subordinates foraged along the forested reaches of the stream and exited the stream after interacting with another bear. However, at mid- to low tide, we often observed subordinate bears in the intertidal areas scavenging dead salmon and in a few cases capturing live fish. During one foraging bout, a subordinate bear spent over 110 min in the intertidal area and consumed parts of 26 senescent dead salmon while a dominant bear captured live salmon in the forested sections of the stream. Senescent dead salmon are much lower in energy content than live ripe salmon (Hendry and Berg 1999; Gende 2002; Gende et al. 2004) but require little effort to obtain.

As subdominant bears foraged for shorter periods and had intake rates half those of dominant bears, the question becomes whether these bears would have done better foraging on alternative food sources, such as berries. Even subordinate bears (lost 100% of interactions) were able to capture a salmon after searching for only a few minutes, resulting in intake rates of about 21 000 kJ during an average of 19 min of foraging, or over 1100 kJ/min. A bear feeding on a high-density blueberry (*Vaccinium* spp.) patch (1500 berries/m³), a common understory shrub in our study area, can consume about 30 g/min foraging (Welch et al. 1997). The average energy density of blueberry is 3.35 kJ/g (Welch et al. 1997), yielding an intake rate of 101 kJ/min. Consequently, at the observed salmon densities, intake rates of subordinate bears would be an order of magnitude greater than if feeding on high-density blueberry patches. We thus provide empirical evidence supporting the hypothesis that bears can achieve far greater rates of intake when fishing for salmon than when foraging for berries or herbaceous vegetation (Welch et al. 1997; Rode et al. 2001) and, by extension, achieve larger body sizes and greater reproductive rates than bear populations without access to salmon (Hilderbrand et al. 1999a).

We recognize the inherent difficulties in estimating total daily intake of free-ranging bears at our sites. Our observations occurred primarily during daylight hours (which constituted 17+ h for portions of the salmon run). Social tolerance among bears may increase at night, although females with cubs and subadults were found to forage most often during the day at a stream in coastal British Columbia (Klinka and Reimchen 2002). We had only three observation periods at night, and in all cases, bears rarely visited the stream, similar to black bears at Olsen Creek, Alaska (Frame 1974), and brown bears at McNeil River Falls (Luque and Stokes 1976). Foraging at dawn and dusk was observed but capture rates were similar to those seen during daylight hours.

Finally, coastal populations of brown bears with access to salmon occur at higher densities, have larger litters, and achieve greater body mass than populations without access to salmon, presumably because of elevated nutritional status (Miller et al. 1997; Hilderbrand et al. 1999a). Our data show that within coastal populations of bears, energy intake can vary dramatically among individual bears, and we hypothesize that variability in reproductive rates may mirror these differences in salmon intake, particularly when salmon densities are low. Although we did not collect data on reproductive success relative to social class, there is anecdotal

information consistent with this hypothesis. First, a sub-population of bears in southeastern Alaska does not utilize salmon runs, remaining in the alpine areas all summer, foraging in less productive but presumably safer habitats (Schoen et al. 1986; Hilderbrand et al. 1996). These bears tend to have small litters (L. Beier, Alaska Department of Fish and Game, Juneau, Alaska, personal communication), although sufficient data to make biologically meaningful comparisons have not been collected. However, if this is the case, the consequence of foregoing salmon consumption may be a reduced ability to energetically support larger litters.

Second, even when few salmon were present, dominant bears foraged for longer periods and captured four to six salmon; in several cases, the number of fish killed constituted a sizeable fraction of the total number of fish present in the stream on that day. During these periods, subordinate bears, although not limited by capture efficiency, were limited by the total number of fish available. When the number of spawning fish increased, dominant bears continued to have high levels of intake, and intermediate and subordinate bears were able to capture more salmon, albeit during shorter foraging bouts. High densities of salmon throughout the season may thus allow more bears to achieve a nutritional state sufficient for successful reproduction. In 2000 at Himmel Creek, only a few chum salmon were present on each day, until mid-August when pink salmon arrived. The dominant bear at this site was a large female with two cubs born the previous winter, and she regularly captured three to five chum salmon during each bout, partially consuming the fish and allowing her offspring free access to each carcass. In contrast, a subordinate bear with two yearling cubs visited the stream on several occasions and captured only one salmon. In each case, she consumed the entire fish and often growled and, in several instances, struck one of her offspring when they tried to feed on the fish that she had captured. For the weeks prior to the arrival of pink salmon, the cubs of the dominant female grew visibly larger but the offspring of the subordinate female did not visibly appear to gain mass. On 24 and 26 August, the subordinate bear was observed foraging without her cubs, suggesting that the nutritional stress of low salmon densities may have resulted in death or abandonment of her cubs.

Our example is limited to one observation but may be representative of the mechanism by which reproductive rates are limited because of social dominance. Salmon populations may fluctuate dramatically from year to year because of natural cycles, fishing pressure, or flow regime (Groot and Margolis 1991). The reproductive advantage of social dominance may be most pronounced during seasons when streams in an area have low salmon returns.

More data are needed to address the interaction between salmon density, social dominance, and fitness consequences, particularly because management activities may inadvertently result in altering availability of or access to salmon by bears, which in turn may influence fitness. Given the increasing interest in bear viewing, managers are faced with decisions of how to maximize access for visitors to bear fishing areas while minimizing disturbance to the bears. We emphasize that any activity (such as construction of bear-

viewing platforms) that alters accessibility to salmon may lower reproductive success of subordinates because dominant bears will be able to monopolize salmon resources to a greater degree.

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